Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

The development of the flower and embryogeny of Martynia louisiana

FLORA ANDERSON.

(WITH PLATES 7 AND 8 AND TWENTY-FIVE TEXT FIGURES)

INTRODUCTION

The most common and widely distributed representative of the Martyniaceae in temperate North America is *Martynia louisiana* Mill. Although the literature on the family is chiefly taxonomic, the descriptions are meagre and confusing. All the species have, at some time, been placed in the genus *Martynia*. The ten or more known species comprise three genera, native to the warmer parts of the western hemisphere.

Efforts were made to secure seeds and to grow plants of the different species for comparison, in order, if possible, to work out the taxonomy of the family. Seeds were obtained from seed-houses both in the United States and in England and also from the Bureau of Plant Industry, the University of Texas and the Mississippi Agricultural College.

From seeds secured through the Bureau of Plant Industry, quite a number of plants of *Martynia louisiana* were grown—all the plants producing viable seeds—and one specimen of *Martynia lutea* Lindl. which, although maturing seemingly normal fruit from selfed flowers, produced no viable seeds. Reciprocal crosses of *Martynia lutea* and *Martynia louisiana*, and of *Martynia lutea* and *Martynia fragrans* Lindl. failed.

From seeds furnished by seed-houses, the University of Texas and the Mississippi Agricultural College, quite a number of plants of *Martynia louisiana* and *Martynia fragrans* were grown in Montgomery County, Indiana, during the summers 1915–1919. The two species mentioned above cross very readily, producing in all cases viable seeds. These plants, grown in the open in rich soil and under practically the same conditions, showed very few differences except in the color of the corolla, which is more or less a variable character. The similarity of the plants seems to indicate that they belong to the same species, but more cultures must be studied before this point can be definitely determined.

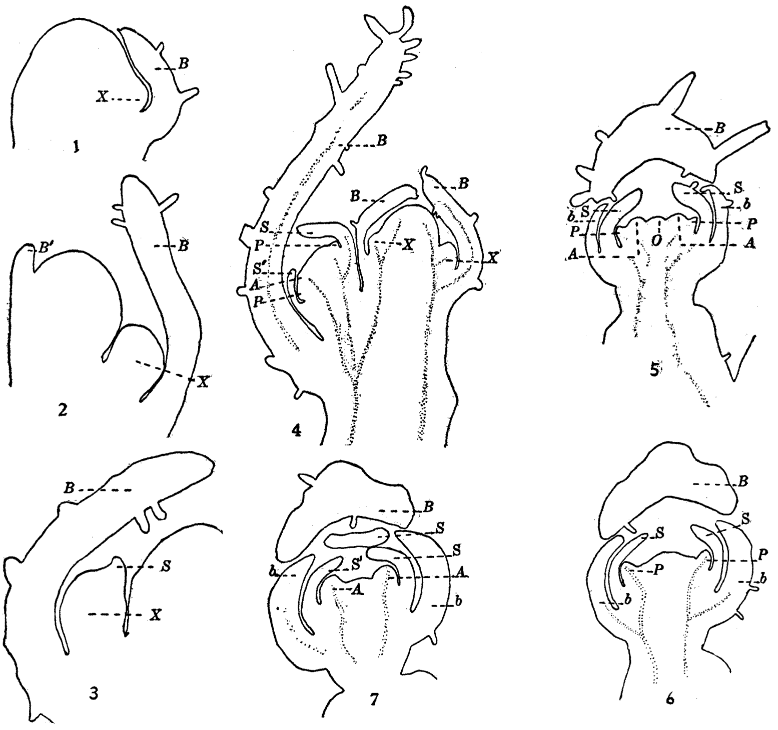
In as much as no morphological work seemed to have been done on this family, a study of *Martynia louisiana* and *Martynia fragrans* was undertaken, the results of which are given in the following pages. While the study was based mainly on *Martynia louisiana* no structural differences between the two species were observed.

MATERIAL AND METHODS

The material used for this study was collected from plants of *Martynia louisiana* and *Martynia fragrans* grown in the field, in Montgomery County, Indiana. Collections were usually made during the month of August, when the plants were most vigorous. The apices of racemes, small flowers and stamens, pistils and young fruits in various stages of development were killed and fixed in a 1 per cent chromo-acetic acid or in chrom-osmic-acetic acid one to two hours and then in chromo-acetic acid twenty-four to thirty-six hours, washed, dehydrated, and embedded through chloroform. To determine the time necessary for the pollen tube to reach the egg, pollination was controlled, and, beginning at one hour after the application of the pollen, collections were made at intervals of one hour for fourteen consecutive hours. These collections were of whole pistils which were killed and fixed in chrom-osmic-acetic acid one to two hours and then in chromo-acetic acid thirty-six hours. Beginning thirty hours after pollination, collections of pistils and young fruits were made at intervals of six hours for two hundred and four hours. Sections were cut 4–10 μ, most of them 5 μ thick; those of whole pistils were longitudinal and 4–5 μ in thickness. Both modified triple and Heidenhain's iron-alum-haematoxylin were used for staining, the former being more satisfactory.

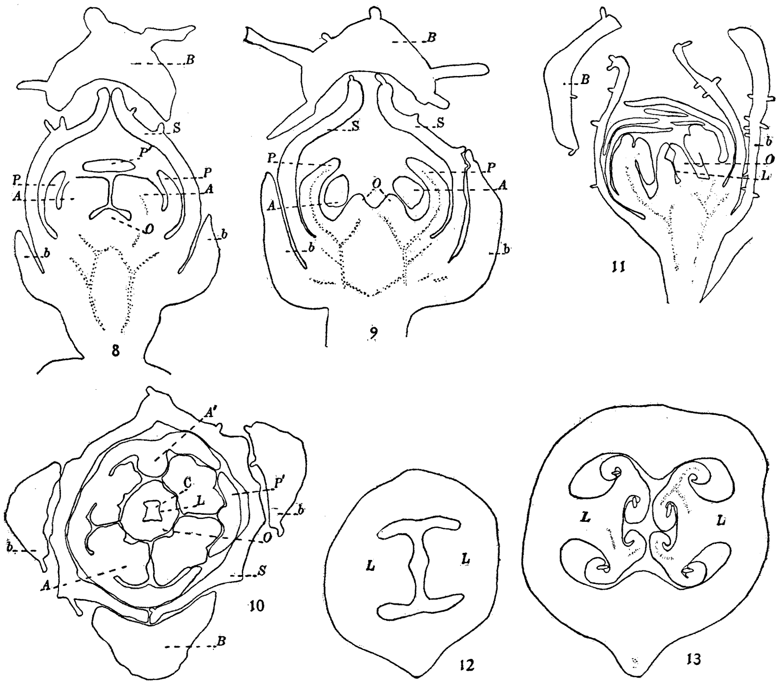
THE DEVELOPMENT OF THE FLOWER

As in most inflorescences, the flower of *Martynia louisiana* arises as a lateral branch (FIG. 1, X) in the axil of a bract (FIG. 1, B). The first bract arises as a lateral papilla near the apex of the main axis of the raceme (FIG. 2, B′). This bract grows rapidly and about the time its tip reaches the apex of the raceme, a rather broad protuberance appears in the axil (FIG. 1, X). With further growth of the axis of the raceme other bracts appear, and in the axils of these the primordia of other flowers develop (FIG. 4, X). As the rudiment of the flower grows it becomes broader and somewhat oblique at the apex (FIGS. 2 and 3, X). On the adaxial side of the primordium of the flower there appears a protuberance or ridge, the upper lobe of the calyx, extending about one third the distance around it (FIG. 3, S). Very soon the other lobes of the calyx appear as small protuberances similar to the adaxial lobe. The individual lobes appear as separate protuberances, but later grow up as a tube except on the abaxial side of the flower. At this point, the two lower lobes of the calyx are united only at the base and in the mature flower overlap. The adaxial lobe of the calyx is the largest, and in the bud covers the other lobes (FIGS. 4 and 7, S). The calyx lobe, shown at S′ in FIG. 4, is the edge of one of the lateral lobes and appears smaller than it really is. Just within the calyx lobes are seen small



FIGS. 1–7. Development of the flower. FIGS. 1–3, × 45; FIGS. 3–7, × 30. B, bract; X, flower primordium; S, S', calyx lobe; P, corolla lobe; A, stamen; O, pistil; b, bracteole.

protuberances (FIG. 4, P), the primordia of the corolla lobes, which are alternate with those of the calyx. Arising simultaneously with the corolla lobes (FIG. 5, P) and alternate with them are the epipetalous stamens (FIG. 5, A). FIGS. 6 and 7 are other sections of the flower shown in FIG. 5. FIG. 6 is a median section through the primordia of two lobes (P) of the corolla, while FIG. 7 is a median section through the primordia of two stamens (A). A comparsion of these two figures will give the relative size of the parts at this stage. There are primordia of five stamens, but very early the one between the posterior pair becomes aborted (FIGS. 10 and 14, A′). The pistil is the last cycle to appear, and in FIG. 5 is seen as a broad protuberance (O).

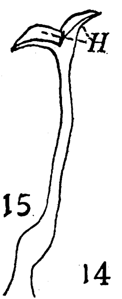


FIGS. 8–13. Development of the flower (*con.*), × 30. B, bract; b, bracteole; S, calyx lobe; P, P^1, corolla lobe; A, A^1, stamen; O, pistil; L, placenta; C, ovarian cavity.

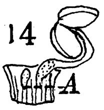
In FIGS. 5–9, at B, are seen cross sections of the bract which curves over the flower. These figures are of the flower as viewed from the adaxial side. And in the same figures at b, are seen sections of the two bracteoles. The two bracteoles arise as protuberances similar to those of the lobes of the calyx, but earlier than the calyx lobes. The bracteoles develop inferior to the calyx, opposite each other and at right angles to the bract (Fig. 10, b, B). Since Fig. 9 is a median section through the flower, only the edge of each bracteole is shown. At this stage, they are large enough to cover the young flower.

Figs. 8 and 9 show the further development of the parts of the flower. The calyx (S) is large enough to cover the other floral parts. An almost median section of two lateral lobes (P) of the corolla is shown in Fig. 9, while a cross section of the tip of the lower lobe is shown at P^1 in Fig. 8. The lower lobe of of the corolla is the largest and in the bud is covered by the others. The manner in which the corolla lobes overlap is shown in Fig. 11. A median section through two of the stamens (Fig. 8, A) of the same flower shows the further development of the stamens seen at A, Fig. 7. As in most cases, the development of the anther precedes that of the filament (Fig. 8, A). However, at this time the tissue of the anther is undifferentiated. At the time the pollen mother-cells are formed the filament is still shorter than the anther. The filaments remain short (Fig. 14) until almost the time of anthesis, when they elongate rapidly, bringing the anthers into the throat of the corolla, just below the lips of the stigma (F.ig 16). The stamens are didynamous, the posterior pair being the longer. Just before anthesis, the lobes of the anther diverge, forming a straight line transverse to the filament. At the same time, the filaments of the corresponding pairs of stamens converge in such a way as to bring the diverging anthers into contact (Fig. 16) along the line of their linear dehiscence. At time of shedding, the rather large pollen grains are characterized by an exine that is thickened in the form of hexagonal areas.

15



14



16

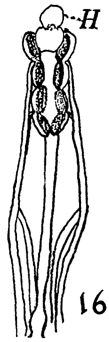


Fig. 14. Immature stamen. A, aborted stamen.

Fig. 15. Mature pistil, slightly enlarged. H, stigma lobes.

Fig. 16. Mature pistil and stamens in position. H, stigma lobes.

As was stated previously, the pistil appears as a rather broad protuberance (Fig. 5, O), but soon a depression is formed in the center (Fig. 9, O). The primordium of the pistil continues to grow up as a ring enclosing a central ovarian cavity as is seen in cross section (FIG. 10, C). At a very early stage in the growth of the pistil, two parietal placentae appear. These are seen as outgrowths from the walls of the cavity (FIGS. 10 and 11, L). These outgrowths extend toward the center of the cavity and soon each forms two lobes (FIG. 12, L) which develop into the two lamellae of each placenta, resembling in cross section the letter T (FIG. 13, L). The placentae grow together at the base, thus forming a short columella. A cross section through the base of the ovary would appear as two-celled, but no ovules are developed from this region of the placentae. The upper part of the pistil is tubular and more narrow, forming a long, slender, hollow style which terminates in an unequally two-lipped stigma (FIG. 15, H).

DEVELOPMENT OF MEGASPORE AND EMBRYO-SAC

The young ovule first appears as a small, nipple-like protuberance upon the placenta. Very early in its development, a hypodermal cell near the tip becomes differentiated and may be distinguished from the surrounding cells by its large nucleus and dense cytoplasm (PLATE 7, FIG. 17). This cell, the megaspore mother-cell, grows rapidly, keeping pace with the lengthening nucellus. At this stage, the nucellus consists of merely the enlarged megaspore mother-cell, covered by the epidermis (FIG. 18). At the base of the nucellus the single integument appears as a fold, at first more pronounced on the side next to the cavity of the ovary (FIG. 18, I). By the more rapid growth of this side the ovule soon becomes sharply curved, so that the long axis of the nucellus is now parallel with that of the funiculus. At this stage, the integument extends around the nucellus, which has become more elongated (FIG. 19). With further growth the integument soon equals and finally exceeds the nucellus (FIGS. 20 and 21). The megaspore mother-cell has also grown rapidly and when fully developed is still enclosed by only a single layer of nucellus (FIG. 21). The nucleus, which has increased in size preparatory to the first division and which has had a position near the center of the cell (FIG. 20), comes to lie nearer the chalazal end, where it undergoes the first or heterotypic division (FIG. 21). All the spindles of this stage found were rather small as compared with the size of the cell. Whether cell formation follows this first nuclear division was not ascertained, but the typical axial row of four megaspores is finally formed (FIG. 22), and, as is usually the case, the innermost megaspore, the one next the chalazal end, persists to form the embryo-sac (FIGS. 22 and 23). The upper three potential megaspores are soon destroyed by the rapid growth of the functional one (FIG. 23.)

By the time the tetrad is formed, the nucellus has reached its maximum growth, and the cells of the integument adjacent to the nucellus have become dense in cytoplasm and now function as a nutritive jacket (FIG. 22). In the meantime the integument has grown and exceeds considerably the length of the nucellus (FIG. 23).

The functional megaspore does not increase much in size before the first nuclear division but, after this first division, it elongates rapidly and occupies a space almost the length of the nucellus (FIGS. 23 and 24). As the megaspore elongates the two nuclei keep their relative positions—one in each end of the cell. Most of the cytoplasm of the cell is in the ends, thus leaving a large vacuole in the center. A few strands of cytoplasm penetrate the vacuole and form a connection between the masses at each end of the cell. The rapid growth of this cell has consumed the three upper potential megaspores and the nucellus around the center of the spore (FIG. 24). Before the second nuclear division of the megaspore takes place, the upper three megaspores have practically disappeared and the functional one now extends nearly the length of the nucellus, which is rapidly being used as food (FIG. 25). At this time the central vacuole is not so pronounced—at least in some cases. The spindles of the second nuclear division may be seen—one in each end of the cell. With the exception of a few cells at the chalazal end, the nucellus is consumed by the growing megaspore, which comes to occupy the space left by the disorganizing tissue. There is no evidence of a nucellar cap being formed as Merrell reported for *Silphium* (**3**) and other plants that have a similar development. The nuclei now undergo another division which results in eight nuclei—four in each end of the cell. Next follows the formation of the three cells of the egg-apparatus and the three antipodals. One nucleus from each end of the embryo-sac, the polar nuclei, remains free in the cytoplasm. At this stage, the embryo-sac is considerably elongated, being about seven times as long as wide. The micropylar end, containing the egg-apparatus, is enlarged to about one and a half times the diameter of the other part of the sac. This enlarged portion comprises nearly one third the length of the embryo-sac. The egg-apparatus consists of the large pear-shaped egg-cell, which extends far down into the sac cavity, and the two large synergids (PLATE 8, FIG. 26, G and Sn). The lower part of the egg in which the nucleus lies is well filled with cytoplasm, but the upper part is vacuolate. The synergids, one on either side of the egg, extend down about two thirds the length of the egg-cell. Each synergid has a diameter nearly equaling that of the egg and a centrally located nucleus, which is a little smaller than the egg nucleus. As is frequently found in other angiosperms, a fairly large vacuole lies below the nucleus in the synergid (FIG. 26, Sn).

In the chalazal end of the embryo-sac are the three, rather long, slender, well-developed antipodals (FIG. 26, N). In most instances, the nuclei of the antipodals are fairly large and the cytoplasm has the character of that of the body of the embryo-sac.

After the formation of the cells at either end of the embryo-sac the polar nuclei move to the center and lie side by side for some time (FIG. 26, Pn), but before the pollen tube reaches the embryo-sac, the two polar nuclei fuse (FIG. 27). Sections were made of ovaries from flowers in which pollination had not occurred and it was found that the polar nuclei had fused (FIG. 28). So the fusion of the polar nuclei is in no way due to a stimulus from the pollen tube. The fusion nucleus does not approach the egg-apparataus, as Kanda reported for *Verbena* (**2**), but remains in the center of the embryo-sac. Each polar nucleus has a very prominent nucleolus and after fusion the two nucleoli are very noticeable for some time (FIG. 27), but later only one large nucleolus is usually seen (FIG. 28).

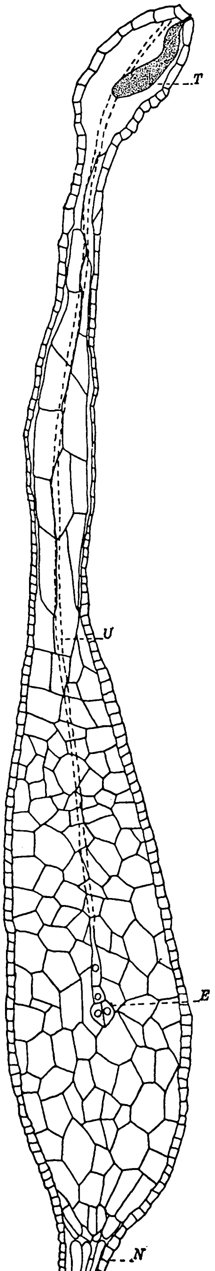
POLLINATION

The polar nuclei seem to unite about the time of anthesis, for conditions like those represented in FIG. 26 are observed in ovaries fixed just before the expansion of the corolla lobes, while the fusion nucleus is seen in flowers that have been open one or two hours. Most of the flowers open early in the morning, and shortly after daylight the bees, which are the chief pollinizing agents, are busy gathering nectar from the lower portion of the corolla tube.

The two lobes of the sensitive stigma stand open just above the open anthers (FIG. 16), in the upper portion of the throat of the corolla, and the bee, entering the corolla tube, brushes the stigma, thus depositing the pollen that may be present on the upper part of its body and securing a new supply from the open anthers just below as it walks down the tube. The stigma is very sensitive when the flower first expands and the slightest touch will cause the lobes to close. If pollen be present they usually remain closed, but, in the absence of pollen, they reopen in from five to ten minutes. If pollen is witheld the stigma lobes may be made to close and open many times, but after one to three days the stigmas tend to lose their sensitiveness. However, this sensitiveness is not an index to the receptiveness of the stigmatic surface, for flowers hand pollinated after the stigma ceased to be sensitive and even after the corolla dropped, produced viable seeds. Viable seeds were also secured from flowers hand pollinated in the bud before the stigma lobes normally opened. This was accomplished by gently forcing pollen between the closed lobes by means of a needle. In most flowers thus treated the stigma lobes never opened. At this time the anthers are still closed, but pollen from these as well as from open anthers was shown to be effective.

FERTILIZATION

Usually the pollen grains germinate immediately on the stigmatic surface, as was readily seen in material fixed one hour after the pollen was applied. At this time, many of the tubes were well into the tissue of the style. The growth of the pollen tube through the tissue, usually two or three cells from the stylar canal, is very rapid, for fertilization frequently occurs within six hours after pollination. The pollen tube is filled with plastids and granules that take such a dense stain that it is impossible to demonstrate the presence of the sperm nuclei, but, since the long, slender crescentic generative cell in the mature pollen grain shows only one nucleus, it is thought that the formation of the two sperms takes place in the tube. The pollen tube, as it grows nearly straight down through the style to the placenta, is comparatively broad and seems to retain its densely staining quality throughout the greater part of its length.



On reaching the ovule, the pollen tube grows through the micropyle and enters the embryo-sac, sometimes a little to one side, crushing one or both the synergids. The tip of the pollen tube usually covers the egg-cell, thus obscuring the nucleus of the latter (FIG. 32). In some instances it seems that the tube enters the egg-cell at the upper end and transverses the entire length of it (FIG. 31). In all cases observed, there was evidence that the tube had discharged the sperm nuclei in such a way that one of them came in direct contact with the egg nucleus (FIG. 30). Only the sperms and a little of the contents from the tip leave the pollen tube (FIGS. 30 and 31). The fate of the second sperm nucleus was not ascertained, but it seems evident that it plays no part in the formation of the endosperm. The second sperm nucleus may not leave the tube, but this point can not be demonstrated until some method of fixing and staining can be found that will reveal the presence of the nuclei among the granules in the cytoplasm. The pollen tube in the micropyle and in the upper part of the embryo-sac retains its form and densely staining quality long after the embryo-sac is filled with endosperm (FIG. 35).

The actual union of sperm and egg nucleus is similar to that in other angiosperms. The instances of fertilization observed were similar to that of *Lilium Martagon*, figured by Mottier (4). For *Verbena*, Kanda (2) figures the sperm nucleus in contact with the egg-cell and speaks of it as fertilization. In all the fertilization stages observed in *Martynia*,

FIG. 35. Embryo-sac filled with endosperm, × 140. T, pollen tube; N, antipodali; E, embryo; U, suspensor.

the sperm has been in direct contact withthe egg nucleus. This would seem to indicate that the pollen tube carries the sperm into the egg-cell.

THE ENDOSPERM

The primary endosperm nucleus, resulting from the union of the two polar nuclei, occupies a position near the center of the embryo-sac. Usually before the pollen tube enters the sac this endosperm nucleus divides and a transverse wall is formed between the two resulting nuclei, thus dividing the embry-sac into two chambers (FIG. 29). At this time, the cytoplasm in the embryo-sac has a frothy appearance due to the many small vacuoles present. This frothy character seems to appear after the fusion of the polar nuclei (FIG. 28). Very conspicuous, densely staining plastid primordia and granules are present in the cytoplasm. The synergids seem to have increased in length and to have become more vacuolate (FIG. 29). The egg-cell remains apparently unchanged. The antipodals are more elongated and sometimes contain a granular, densely staining cytoplasm (FIG. 29). After the wall dividing the embryo-sac into two chambers is formed, the nuclei move to a nearly central position in their respective cells. And, as one would infer, the endosperm cell at the micropylar end of the sac grows more rapidly than the one at the chalazal end (FIG. 31). The pollen tube usually reaches the embryo-sac when the endosperm is in a two-celled stage. In FIG. 31, it may be seen that fertilization has taken place. The outline of the tip of the pollen tube is shown by a dotted line in the lower part of the egg-cell, and the shading represents the relative density of the contents in different parts of the tube. Only the tip seems to have discharged its contents. A remnant of one synergid still shows. The synergids, if not crushed out by the entrance of the pollen tube, are soon absorbed. The endosperm cell in the micropylar end of the sac is very large and contains a large nucleus with irregular outline and a prominent nucleolus. Many plastids are still seen in the frothy cytoplasm of both endosperm cells, and some are present in the antipodals, which continue to grow, especially in length (FIG. 31). The increase in size of the antipodals is better illustrated in FIG. 32. Their cytoplasm is somewhat vacuolate at this stage and the large nuclei contain very prominent nucleoli. Usually the first division of the endosperm cell is transverse and the second longitudinal, the one in the micropylar end dividing before the one in the chalazal end; but, in FIG. 32, it appears as if the first division had been longitudinal and the second transverse. The cytoplasm in the large cells around the fertilized egg contains many large as well as small vacuoles, while that of the lower cells contains only small ones. Very few plastids are present at this stage. They are seldom noticeable in later stages of endosperm development. FIG. 32 shows also the old densely staining pollen tube in the micropyle and upper end, of the embryo-sac, its tip covering the fertilized egg. By focusing down on the tip of the tube, the nucleus of the fertilized egg is seen and is represented in the drawing by a dotted line (FIG. 32). In the meantime, the whole embryo-sac has been enlarging at the expense of the integument which also has grown. The enlargement is more pronounced at first in the micropylar end where the fertilized egg is elongating. The layer of cells of the integument adjacent to the embryo-sac is always dense and rich in cytoplasm and functions as a nutritive jacket to the growing endosperm. FIG. 33 shows the further development of the endosperm, and the elongation of the fertilized egg. The old pollen tube is still very prominent in the micropyle and upper end of the sac, obscuring the upper portion of the fertilized egg-cell. The cytoplasm in the large endosperm cells of the micropylar end is very vacuolate, due probably to the rapid growth of the cells and to the loss of food to the developing embryo. Only a few endosperm cells develop in this end of the sac, for very soon a long suspensor is formed which brings the embryo into the chalazal end. The endosperm cells in the middle of the sac are smaller and richer in cytoplasm than the upper ones. The antipodals have nearly reached their maximum growth. They seem to function as elaborators of food and persist long after the embryo-sac is well filled with endosperm (FIG. 35). In several cases, four antipodals, all well developed, were found (FIG. 33). The extra one had probably been formed by the

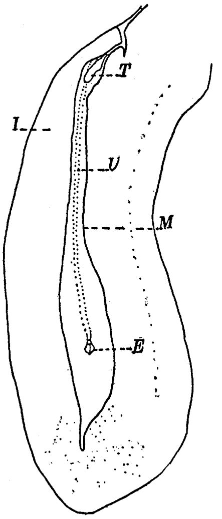


FIG. 36. Outline of ovule, × 44. I, integument; M, embryo-sac E, embryo; U, suspensor; T, old pollen tube.

division of one of the three normal ones. FIG. 34, a cross section of the chalazal end of an embryo-sac in the same stage as the above, shows the arrangement of the four antipodals. At this stage, the nuclei of the antipodals appear as densely staining homogeneous masses.

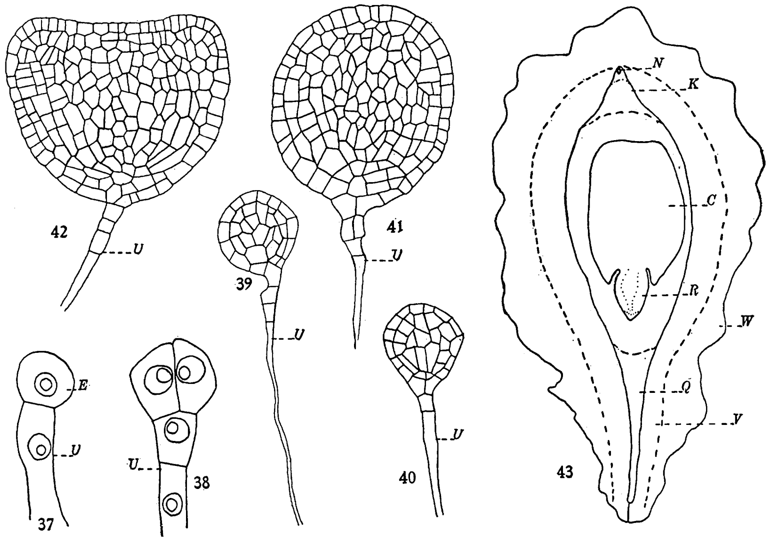
As the embryo with its very long suspensor grows through the center of the elongating embryo-sac, large endosperm cells rich in cytoplasm are formed, but when it reaches the lower part of the sac where the first division of the embryo takes place, the endosperm growth practically ceases in the middle and upper part of the sac. The cells of this part of the sac are rather large and similar in shape to those first formed, while those in the lower part are smaller and not so rich in cytoplasm (FIG. 35). It is also seen from FIG. 35 that the embryo-sac has enlarged considerably, especially the lower part which contains the developing embryo. The nutritive jacket is still very active in the elaboration of food for the growing endosperm. FIG. 36 shows in outline the relative size of the embryo, endosperm and integument at the time the embryo is in the two-cell stage as seen in FIG. 35.

THE EMBRYO

After fertilization, the egg with its nucleus occupying a nearly central position in the lower part of the cell grows rapidly in length (FIG. 33). Its manner of growth down through the endosperm is similar to that of a pollen tube, for it becomes a long narrow cell with the nucleus retaining a position near the growing tip. No division seems to take place until the distal end has transversed nearly two thirds the length of the embryo-sac. The lower portion of the cell is rather dense in cytoplasm and stains deeply, but the upper portion has very little and stains so faintly that the course of its growth is hard to trace.

After the distal end has reached the lower portion of the embryo-sac, a transverse division occurs, which forms a very long, slender suspensor cell and a short, rounded distal one, the embryonal cell (FIG. 37). In most instances the cytoplasm of the embyonal cell contains many plastids and other densely staining granules, while that of the suspensor is very poor in plastids. After the first division two others occur almost simultaneously. The suspensor cell divides, forming a short cell next the embryonal cell, which has enlarged preparatory to division, and, at the same time, the enlarged embryonal cell divides longitudinally forming a two-celled embryo (FIGS. 38 and 35). The second division of the embryo is usually transverse and the third longitudinal, thus forming the octant stage The further growth of the embryo is illustrated in FIGS. 39–43 and is so like the well known development of *Capsella* that details are unnecessary.

The very long suspensor, shown in Fig. 35 in dotted lines, is almost indentical with that of *Trapella sinensis* Oliv. as figured by Oliver (**5**, *pl. 7, f. 36*). The suspensor of *Myoporum* *serratum* as figured by Billings (**1**, *f. 51*) is also similar in structure but does not push the embryo as far down into the embryo-sac as that of *Martynia*, although the shape of the embryo-sac and the development of the endosperm are much the same in both species. Usually a second and sometimes a third division occurs in the suspensor, resulting in two or three short cells next the embryo, the innermost of which seems to contribute to its formation.



FIGS. 37–43. Development of the embryo. FIGS. 37–38, × 500; FIGS. 39–42, × 175; FIG. 43, × 6. E, embryo; U, suspensor; C, cotyledon; R, radicle; K, chalazal end of embryo-sac; Q, micropylar end of embryo-sac; N, remains of antipodals; V, soft, inner portion of seed coat; W, hard, warty portion of seed coat.

FIG. 43 shows a section of a young seed containing a nearly mature embryo. The radicle (R) is short and thick while the cotyledons (C) are very large and fleshy. This figure shows also a little endosperm which, in the mature seed, comprises a thin, transparent covering for the embryo. The embryo has developed in such a way that it practically fills the lower part of the sac, while the upper and middle portions (Q) form in the mature seed a little brown tube on the micropylar end of the remaining endosperm. There is also a small brown knob at the chalazal end (K) marking that part of the embryo-sac formerly occupied by the large antipodals, the remains of which appear at N. The broken line in this figure represents the demarcation in the tissue forming the seed coat. That region of tissue next the endosperm (V) matures into the soft inner portion of the seed coat, while the walls of the cells forming the outer portion (W) become thick and lignified, thus maturing into a hard warty exterior which becomes very dark brown or black in color.

SUMMARY

The flowers develop in the axils of protective bracts. The cycles of the flower appear in the following order: calyx, corolla and epipetalous stamens, and pistil.

Of the four potential megaspores formed, only one is functional.

The embryo-sac is long and narrow, with the micropylar end considerably enlarged. The large egg-cell extends far down into the sac cavity, with the two synergids on either side. The three antipodals are long, slender cells that increase in size and persist as elaborators of food.

The polar nuclei move to a position near the center of the sac where they unite before the pollen tube reaches the ovule.

Fertilization usually occurs within six to eight hours after pollination.

The rather large pollen tube stains densely throughout the greater part of its length and persists in the micropyle and upper end of the embryo-sac long after the endosperm is formed.

The first division of the endosperm cell, which is usually transverse, occurs before fertilization. At first, a few cells are formed in the upper and middle portions of the embryo-sac, but the bulk of the endosperm is in the lower part of the sac, where the embryo develops.

The suspensor is very long and narrow and pushes the embryo into the lower portion of the embryo-sac, where the first division takes place. The development of the embryo proper is like that of *Capsella*.

I take opportunity here to express my obligations to Professor H. W. Anderson for the use of the Wabash College Botanical Laboratory during the summers of 1915 and 1916 and to Professor D. M. Mottier for valuable assistance and criticism in connection with this study.

INDIANA UNIVERSITY

LITERATURE CITED

1. **Billings, Frederick H.** Beiträge zur Kenntniss der Samenentwickelung. Flora **88**: 253–318. 1902.
2. **Kanda, M.** Field and laboratory studies of *Verbena*. Bot. Gaz. **69**: 54–71. *pl. 6–9* + *f. 10–17, 27, 54–63, 69–75*. 1920.
3. **Merrell, W. D.** A contribution to the life history of *Silphium*. Bot. Gaz. **29**: 99–133. *pl. 3–10*. 1900.
4. **Mottier, D. M.** Fecundation in plants. Carnegie Inst. Washington Publ. 15. 1904.
5. **Oliver, F. W.** On the structure, development, and affinities of *Trapella*, Oliv., a new genus of Pedalineae. Ann. Bot. **2**: 75–115. *pl. 5–9*. 1888.

Explanation of plates 7 and 8

PLATE 7

All figures, × 400

FIG. 17. Vertical section through the nucellus; megaspore mother-cell shaded.

FIG. 18. Elongated nucellus with megaspore mother-cell; beginning of integument, I.

FIG. 19. Vertical section of young ovule turned on its axis; the integument reaching half the length of the nucellus.

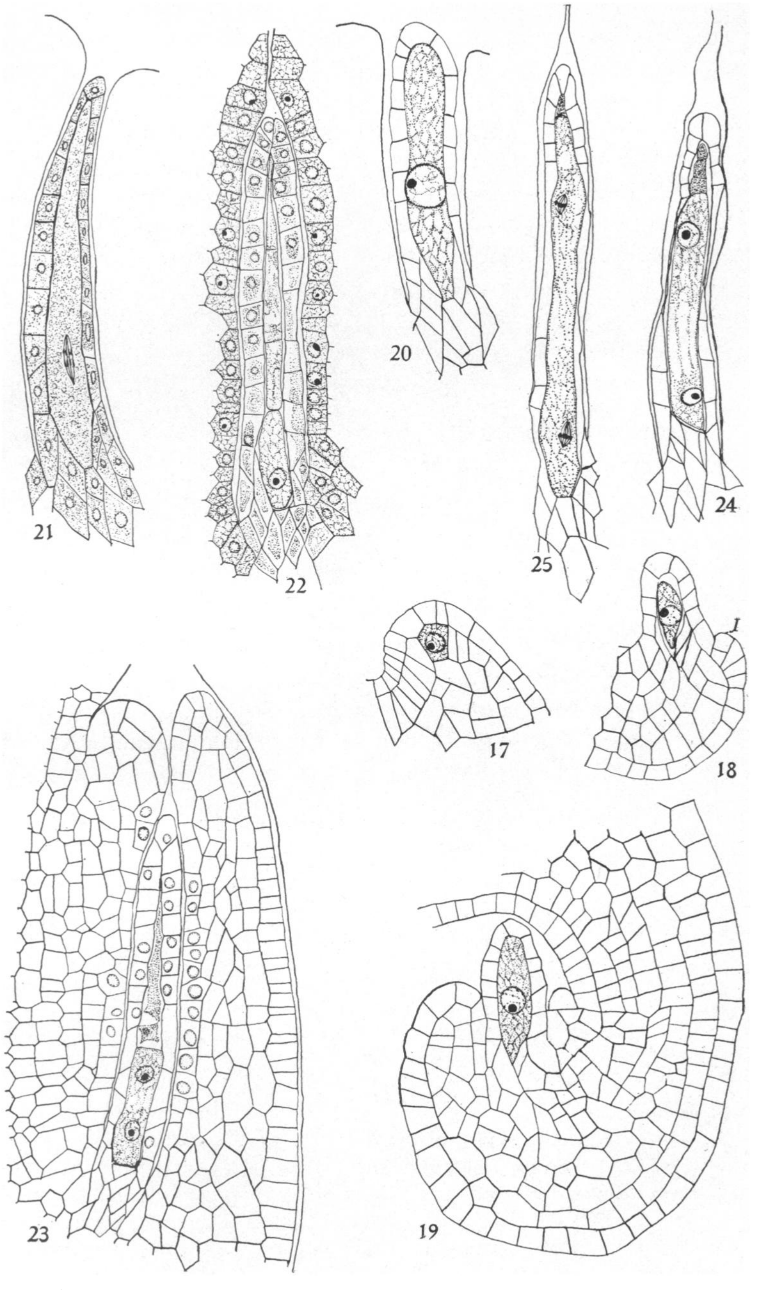
FIG. 20. Nearly mature megaspore mother-cell enclosed in a single layer of nucellus.

FIG. 21. Heterotypic spindle in megaspore mother-cell.

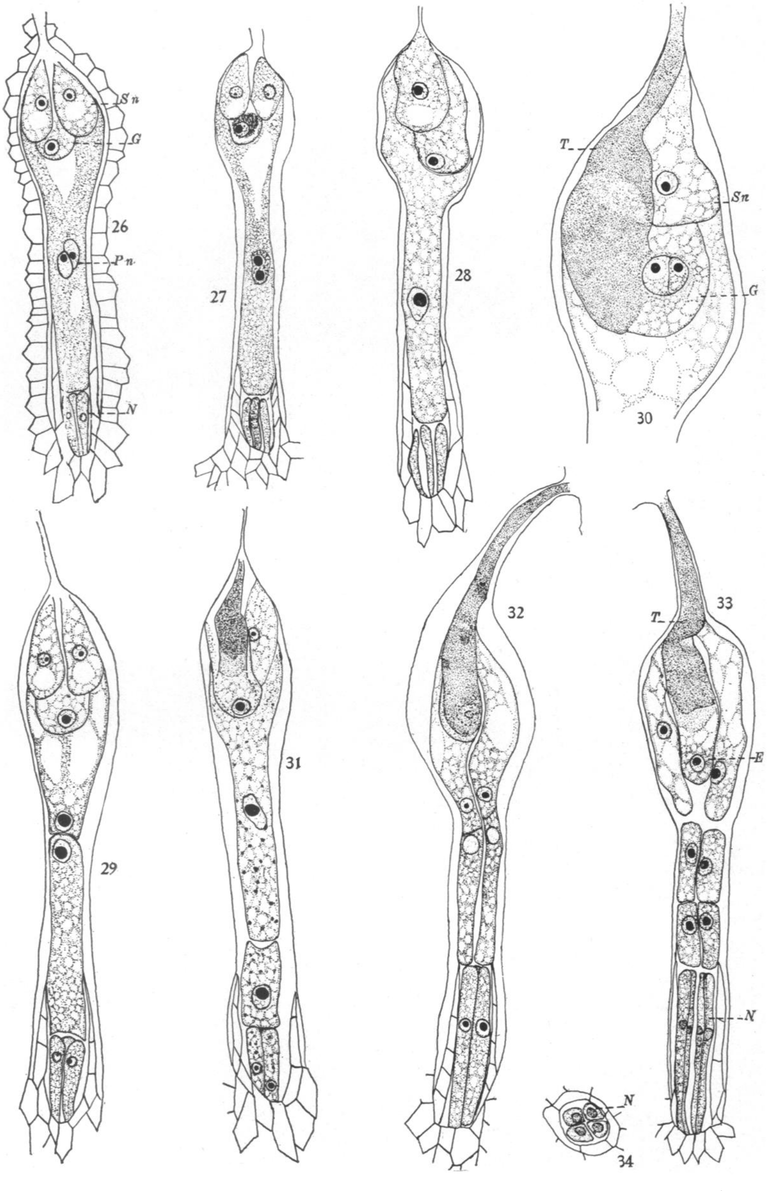
FIG. 22. Tetrad, the upper three potential megaspores disorganizing. Nutritive jacket formed from the layer of integument adjacent the nucellus.

FIG. 23. Section of young ovule showing the single integument and first division of the megaspore; the upper three potential megaspores disorganizing.

FIGS. 24 and 25. Further development of the megaspore; the central portion of nucellus disorganizing.



ANDERSON: FLOWER AND EMBRYOGENY OF MARTYNIA



ANDERSON: FLOWER AND EMBRYOGENY OF MARTYNIA

PLATE 8

FIGS. 26–33, longitudinal sections of embryo-sacs. FIG. 34, cross section of antipodals.

FIG. 26. Mature embryo-sac; polar nuclei side by side near the center of the sac; G, egg-cell; Sn, synergid; N, antipodals; Pn, polar nuclei, × 300.

FIG. 27. Mature embryo-sac; polar nuclei fusing, × 300.

FIG. 28. Mature embryo-sac; polar nuclei fused, × 350.

FIG. 29. Endosperm two-celled; egg not yet fertilized, × 350.

FIG. 30. Fertilization. Sperm and egg nuclei in contact; old pollen tube quite prominent; G, egg-cell; T, pollen tube; Sn, synergid, X 740.

FIGS. 31 and 32. Development of endosperm and elongation of antipodals, X 350.

FIG. 33. Development of endosperm and embryo; four antipodals, N; E, elongating embryo; T, old pollen tube, × 350.

FIG. 34. Cross section of chalazal end of embryo-sac showing four antipodals, N, × 350.